PHILOSOPHICAL

TRANSACTIONS.

XI. *Account of some Experiments on the Descent of the Sap in Trees. In a Letter from* Thomas Andrew Knight, *Esq. to the Right Hon. Sir* Joseph Banks, *Bart. K. B. P. R. S.*

Read April 21, 1803.

MY DEAR SIR,

In a Memoir which I had the honour to present to you two years ago,* I related some experiments on trees, from which I inferred, that their sap, having been absorbed by the bark of the root, is carried up by the alburnum or white wood, of the root, the trunk, and the branches; that it passes through what are there called the central vessels, into the succulent part of the annual shoot, the leaf-stalk, and the leaf; and that it returns to the bark, through the returning vessels of the leaf-stalk. The principal object of this Paper is, to point out the causes of the descent of the sap through the bark, and the consequent formation of wood.

These causes appear to be, gravitation, motion communicated

* See Phil. Trans. for 1801, p. 333.

by winds or other agents, capillary attraction, and probably something in the conformation of the vessels themselves, which renders them better calculated to carry fluids in one direction than in another. I shall begin with a few observations on the leaf, from which all the descending fluids in the tree appear to be derived. This organ has much engaged the attention of naturalists, particularly of M. BONNET: but their experiments have chiefly been made on leaves severed from the tree; and, therefore, whatever conclusions have been drawn, stand on very questionable ground. The efforts which plants always make to turn the upper surfaces of their leaves to the light, have with reason induced naturalists to conclude, that each surface has a totally distinct office; and the following experiments tend strongly to support that conclusion.

I placed a small piece of plate glass under a large vine leaf, with its surface nearly parallel with that of the leaf; and, as soon as the glass had acquired the temperature of the house in which the vine grew, I brought the under surface of the leaf into contact with it, by means of a silk thread and a small wire, adapted to its form and size. Having retained the leaf in this position one minute, I removed it, and found the surface of the glass covered with a strong dew, which had evidently exhaled from the leaf. I again brought the leaf into contact with the glass, and, at the end of half an hour, found so much water discharged from the leaf, that it ran off the glass when held obliquely. I then inverted the position of the leaf, and placed its upper surface in contact with the glass: not the slightest portion of moisture now appeared, though the leaf was exposed to the full influence of the meridian sun. These experiments were repeated on many different leaves; and the result was, in

every instance, precisely the same. It seems, therefore, that in the vine, the perspiratory vessels are confined to the under surface of the leaf: and these, like the cutaneous lymphatics of the animal economy, are probably capable of absorbing moisture, when the plant is in a state to require it. The upper surface seems, from the position it always assumes, either formed to absorb light, or to operate by the influence of that body; and, if any thing exhale from it, it is probably vital air, or some other permanently elastic fluid. It nevertheless appears evident, in the experiments of BONNET, that this surface of the leaves of many plants, when detached from the tree, readily absorbs moisture.

Selecting two young shoots of the vine, growing perpendicularly against the back wall of my vinery, I bent them downwards, nearly in a perpendicular line, and introduced their succulent ends, as layers, into two pots, without wounding the stems, or depriving them of any portion of their leaves. In this position, these shoots, which were about four feet long, and sprang out of the principal stem about three feet from the ground, grew freely, and, in the course of the summer, reached the top of the house. As soon as their wood became sufficiently solid to allow me to perform the operation with safety, I made two circular incisions through the bark of the depending part of each shoot, at a small distance from each other, near the surface of the mould in the pots; and I wholly removed the bark between the incisions; thus cutting off all communication, through the bark, between the layers and the parent stems. Had the subjects of this experiment now retained their natural position, much new wood and bark would have been formed at the upper lip of the wounds, and none at all at the lower, as I

have ascertained by frequent experiment. The case was now different: much new bark and wood was generated on the lower lip of the wounds, become uppermost by the inverted position of the branches; and I have no doubt but that the new matter, thus deposited, owed its formation to a portion of sap, which descended by gravitation, from the leaves growing between the wounded parts and the principal stems.

The result of this experiment appears to point out one of the causes why perpendicular shoots grow with much greater vigour than others: they have probably a more perfect and more rapid circulation.

The effects of motion on the circulation of the sap, and the consequent formation of wood, I was best able to ascertain by the following expedient. Early in the spring of 1801, I selected a number of young seedling apple-trees, whose stems were about an inch in diameter, and whose height, between the roots and first branches, was between six and seven feet. These trees stood about eight feet from each other; and, of course, a free passage for the wind to act on each tree was afforded. By means of stakes and bandages of hay, not so tightly bound as to impede the progress of any fluid within the trees, I nearly deprived the roots and lower parts of the stems, of several trees, of all motion, to the height of three feet from the ground, leaving the upper parts of the stems and branches in their natural state. In the succeeding summer, much new wood accumulated, in the parts which were kept in motion by the wind; but the lower parts of the stems and roots increased very little in size. Removing the bandages from one of these trees in the following winter, I fixed a stake in the ground, about ten feet distant from the tree, on the east side of it; and I attached the

tree to the stake, at the height of six feet, by means of a slender pole about twelve feet long; thus leaving the tree at liberty to move towards the north and south, or, more properly, in the segment of a circle, of which the pole formed a radius; but in no other direction. Thus circumstanced, the diameter of the tree from north to south, in that part of its stem which was most exercised by the wind, exceeded that in the opposite direction, in the following autumn, in the proportion of thirteen to eleven.

These results appear to open an extensive and interesting field to our observation, where we shall find much to admire, in the means which nature employs to adapt the forms of its vegetable productions to every situation in which art or accident may deposit them. If a tree be placed in a high and exposed situation, where it is much kept in motion by winds, the new matter which it generates will be deposited chiefly in the roots and lower parts of the trunk; and the diameter of the latter will diminish rapidly in its ascent. The progress of the ascending sap will of course be impeded; and it will thence cause lateral branches to be produced, or will pass into those already existing. The forms of such branches will be similar to that of the trunk; and the growth of the insulated tree on the mountain will be, as we always find it, low and sturdy, and well calculated to resist the heavy gales to which its situation constantly exposes it.

Let another tree of the same kind be surrounded, whilst young, by others, and it will assume a very different form. It will now be deprived of a part of its motion, and another cause will operate: the leaves on the lateral branches will be partly deprived of light, and, as I have remarked in the last Paper I

had the honour to address to you, little alburnum will then be generated in those branches. Their vigour, of course, becomes impaired, and less sap is required to support their diminished growth: more, in consequence, remains for the leading shoots; these, therefore, exert themselves with increased energy; and the trees seem to vie with each other for superiority, as if endued with all the passions and propensities of animal life.

An insulated tree in a sheltered valley, will assume, from the foregoing causes, a form distinct from either of the preceding;* and its growth will be more or less aspiring, in proportion to the degree of protection it receives from winds, and its contiguity to elevated objects, by which its lower branches, during any part of the day, are shaded.

When a tree is wholly deprived of motion, by being trained to a wall, or when a large tree has been deprived of its branches, to be regrafted, it often becomes unhealthy, and not unfrequently perishes, apparently owing to the stagnation of the descending sap, under the rigid cincture of the lifeless external bark. I have, in the last two years, pared off this bark from some very old pear and apple-trees, which had been regrafted with cuttings from young seedling trees; and the effect pro-

* Not only the external form of the tree, but the internal character of the wood will be affected by the situation in which the tree grows; and hence, oak timber which grew in crowded forests, appears to have been mistaken, in old buildings, for Spanish chesnut. But I have found the internal organization of the oak and Spanish chesnut to be very essentially different. (See a magnified view of each in Plate IV.) The silver grain and general character of the oak and Spanish chesnut, are also so extremely dissimilar, that the two kinds of wood can only be mistaken for each other by very careless observers. Many pieces of wood found in the old buildings of London, and supposed to be Spanish chesnut, have been put into my hands; but they were all most certainly forest oak.

duced has been very extraordinary. More new wood has been generated in the old trunks, within the last two years, than in the preceding twenty years; and I attribute this to the facility of communication which has been restored between the leaves and the roots, through the inner bark. I have had frequent occasion to observe, that wherever the bark has been most reduced, the greatest quantity of wood has been deposited.

Other causes of the descent of the sap towards the root, I have supposed to be, capillary attraction, and something in the conformation of the vessels of the bark. The alburnum also appears, in my former experiments, to expand and contract very freely, under changes of temperature and of moisture; and the motion thus produced must be in some degree communicated to the bark, should the latter substance be in itself wholly inactive. I however consider gravitation as the most extensive and active cause of motion, in the descending fluids of trees; and I believe, that from this agent, vegetable bodies, like unorganized matter, generally derive, in a greater or less degree, the forms they assume; and probably it is necessary to the existence of trees that it should be so. For, if the sap passed and returned as freely in the horizontal and pendent, as in the perpendicular branch, the growth of each would be equally rapid, or nearly so: the horizontal branch would then soon extend too far from its point of suspension at the trunk of the tree, and thence must inevitably perish, by the compound ratio in which the powers of destruction, compared with those of preservation, would increase.

The principal office of the horizontal branch, in the greatest number of trees, is to nourish and support the blossoms, and the fruit or seed; and, as these give back little or nothing to the

parent tree, very feeble powers alone are wanted in the returning system. No power at all had been fatal; and powers sufficiently strong wholly to counteract the effects of gravitation, had probably been in a high degree destructive. And it appears to me by no means improbable, that the formation of blossoms may, in many instances, arise from the diminished action of the returning system in the horizontal or pendent branch.

I have long been disposed to believe the ascending fluids in the alburnum and central vessels, wherever found, to be everywhere the same; and that the leaf-stalk, the tendril of the vine, the fruit-stalk, and the succulent point of the annual shoot, might in some measure be substituted for each other; and experiment has proved my conjecture, in many instances, to be well founded. Leaves succeeded, and continued to perform their office, when grafted on the fruit-stalk, the tendril, and succulent shoot, of the vine; and the leaf-stalk, the tendril, and the fruit-stalk, alike supplied a branch grafted upon them with nourishment. But I did not succeed in grafting a fruit-stalk of the vine on the leaf-stalk, the tendril, or succulent shoot. My ill success, however, I here attribute solely to want of proper management; and I have little doubt of succeeding in future.

The young shoots of the vine, when grafted on the leaf-stalk, often grew to the length of nine or ten feet; and the leaf-stalk itself, to some distance below its juncture with the graft, was found, in the autumn, to contain a considerable portion of wood, in every respect similar to the alburnum in other parts of the tree.

The formation of alburnum in the leaf-stalk, seemed to point out to me the means of ascertaining the manner in which it is generated in other instances; and to that point my attention was in consequence attracted. Having grafted a great many

leaf-stalks with shoots of the vine, I examined, in transverse sections, the commencement and gradual formation of the wood. It appeared evidently to spring from the tubes which, in my last Paper, (to which I must refer you,) I have called the returning vessels of the leaf-stalk; and to be deposited on the external sides of what I have there named the central vessels, and on the medulla. The latter substance appeared wholly inactive; and I could not discover any thing like the processes supposed to extend from it, in all cases, into the wood.

The organization of the young shoot is extremely similar to that of the leaf-stalk, previous to the formation of wood within it. The same vessels extend through both; and therefore it appeared extremely probable, that the wood in each would be generated in the same manner: and subsequent observation soon removed all grounds of doubt.

It is well known that, in the operation of budding, the bark of trees being taken off, readily unites itself to another of the same or of a kindred species. An examination of the manner in which this union takes place, promised some further information. In the last summer, therefore, I inserted a great number of buds, which I subsequently examined, in every progressive stage of their union with the stock. A line of confused organization marks the place where the inserted bud first comes into contact with the wood of the stock; between which line and the bark of the inserted bud, new wood regularly organized is generated. This wood possesses all the characteristics of that from which the bud was taken, without any apparent mixture whatever with the character of the stock in which it is inserted. The substance which is called the medullary process, is clearly seen to spring

from the bark, and to terminate at the line of its first union with the stock.

An examination of the manner in which wounds in trees become covered, (for, properly speaking, they never can be said to heal,) affords further proof, were it wanted, that the medullary processes, (as they are improperly named,) like every other part of the wood, are generated by the bark.

Whenever the surface of the alburnum is exposed but for a few hours to the air, though no portion of it be destroyed, vegetation on that surface for ever ceases. But new bark is gradually protruded from the sides of the wound, and by this new wood is generated. In this wood, the medullary processes are distinctly seen to take their origin from the bark, and to terminate on the lifeless surface of the old wood within the wound. These facts incontestibly prove, that the medullary processes, which in my former Paper I call the silver grain, do not diverge from the medulla, but that they are formed in lines converging from the bark to the medulla, and that they have no connection whatever with the latter substance. And surely nothing but the fascinating love of a favourite system, could have induced any naturalist to believe the hardest, the most solid, and most durable part of the wood, to be composed of the soft, cellular, and perishable substance of the medulla.

In my last Paper, I have supposed that the sap acquired the power to generate wood in the leaf; and I have subsequently found no reason to retract that opinion. But the experiment in which wood was generated in the leaf-stalk, apparently by the sap descended from the bark of the graft, induces me to believe, that the descending fluid undergoes some further changes in

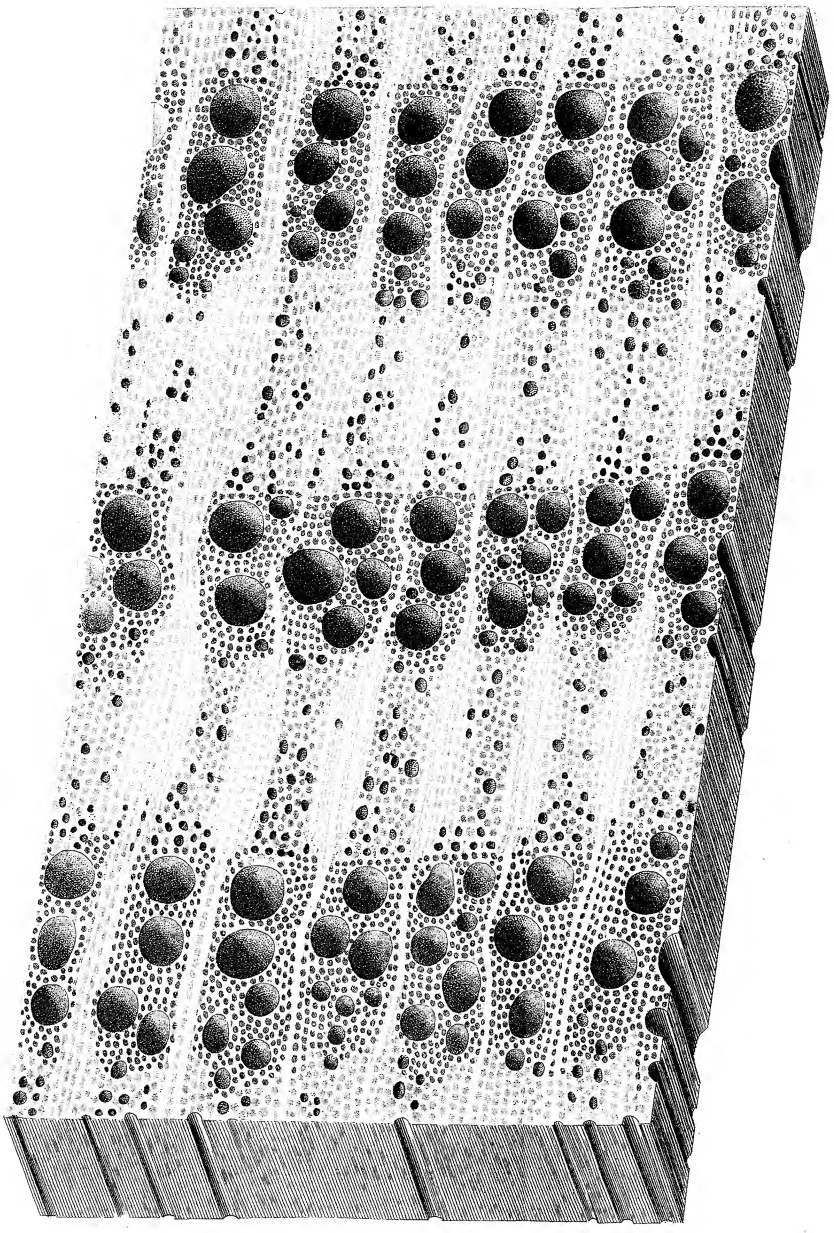
the bark, possibly by discharging some of its component parts through the pores described and figured by MALPIGHI.

I also suspected, since my former Paper was written, that the young bark, in common with the leaf, possessed a power, in proportion to the surface it exposes to the air and light, of preparing the sap to generate new wood; for I found that a very minute quantity of wood was deposited by the bark, where it had not any apparent connection with the leaves. Having made two incisions through the bark round annual shoots of the apple-tree, I entirely removed the bark between the incisions, and I repeated the same operation at a little distance below, leaving a small portion of bark unconnected with that above and beneath it. By this bark, a very minute quantity of wood, in many instances, appeared to be generated, at its lower extremity. The buds in the insulated bark were sometimes suffered to remain, and in other instances were taken away; but these, unless they vegetated, did not at all affect the result of the experiment. I could therefore account for the formation of wood, in this case, only by supposing the bark to possess in some degree, in common with the leaf, the power to produce the necessary changes in the descending sap; or that some matter originally derived from the leaves, was previously deposited in the bark: or that a portion of sap had passed the narrow space above, from which the bark had been removed, through the wood. Repeating the experiment, I left a much greater length of bark between the intersections; but no more wood than in the former instances was generated. I therefore concluded, that a small quantity of sap must have found its way through the wood, from the leaves above; and I found, that when the upper incisions were made at ten or twelve lines distance, instead of

one or two, and the bark between them, as in the former experiments, was removed, no wood was generated by the insulated bark.

I shall conclude my Paper with a few remarks on the formation of buds, in tuberous rooted plants, beneath the ground. They must, if my theory be well founded, be formed of matter which has descended from the leaves through the bark. I shall confine my observations to the potatoe. Having raised some plants of this kind in a situation well adapted to my purpose, I waited till the tubers were about half grown; and I then commenced my experiment by carefully intersecting, with a sharp knife, the runners which connect the tubers with the parent plant, and immersing each end of the runners, thus intersected, in a decoction of logwood. At the end of twenty-four hours, I examined the state of the experiment; and I found that the decoction had passed along the runners in each direction; but I could not discover that it had entered any of the vessels of the parent plant. This result I had anticipated; because I concluded, that the matter by which the growing tuber is fed, must descend from the leaves through the bark; and experience had long before taught me, that the bark would not absorb coloured infusions. I now endeavoured to trace the progress of the infusion in the opposite direction; and my success here much exceeded my hopes.

A section of the potatoe presents four distinct substances: the internal part, which, from the mode of its formation and subsequent office, I conceive to be allied to the alburnum of ligneous plants; the bark which surrounds this substance; the true skin of the plant; and the epidermis. Making transverse sections of the tubers which had been the subjects of the



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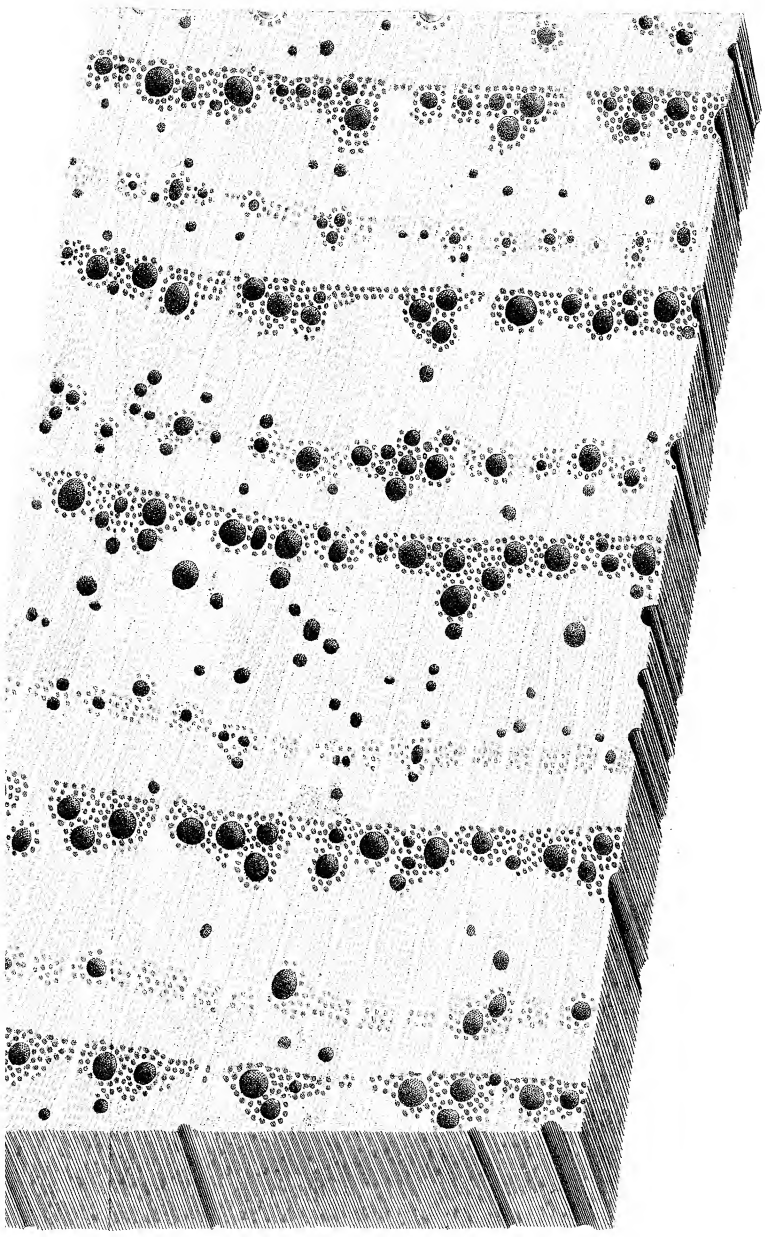

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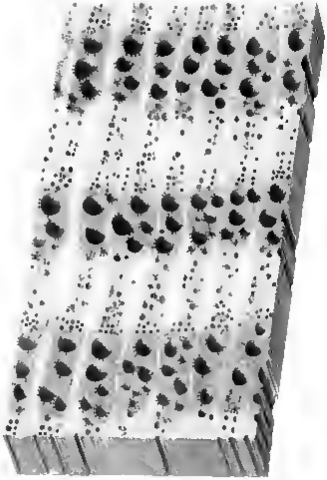
experiments, I found that the coloured infusion had passed through an elaborate series of vessels between the cortical and alburnous substances, and that many minute ramifications of these vessels approached the external skin at the base of the buds, to which, as to every other part of the growing tuber, I conclude they convey nourishment.

Some other experiments were made on this plant, which appeared to me interesting; but my Paper has already a good deal exceeded its intended limits. I will therefore dismiss the subject; but intend to trouble you with another Memoir in the autumn, should this be honoured with the approbation of the Royal Society.

I am, &c.

T. A. KNIGHT.

Elton,
March 26, 1803.



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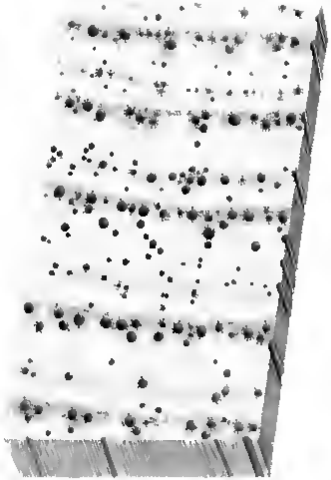

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